



Context-dependent variation of house finch song syntax

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We explored the role of social context in the syntactical variation of house finch, *Haemorhous mexicanus*, songs using both traditional song measures and network analysis. In comparison to solo bouts, the bouts of countersinging males had increased syntax diversity, with higher numbers of simple paths and transition types (but not syllable types) in comparison to solo song, which had high sequence consistency. Both the proportion of introductory syllables and the degree (number of transitions to and from those syllables) increased in countersinging bouts and were an important source of syntactic variability. In contrast, courtship bouts included longer songs and longer syllables than both solo and countersinging bouts, but were similar to solo songs in sequence consistency. The longest courtship songs often included concatenated sequences that formed 'compound songs', or repeating strings of main song syllables, which slightly increased the degree of those syllables. Our results suggest that interactions between males are associated with increased syntactic variability in song delivery while female choice favours signals that maintain species-typical syntax and demonstrate fitness in terms of a male's capacity to sing extended songs.

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The vocalizations of many species consist of syllables delivered in a fixed order. However, some songs have rules for ordering content that are intrinsically variable, and include branching points or subunits that can be freely rearranged to create different sequences. For nightingales, *Luscinia megarhynchos* (Weiss, Hultsch, Adam, Scharff, & Kipper, 2014) and California thrashers, *Toxostoma redivivum* (Cody, Stable, Sánchez Castellanos, & Taylor, 2015), the ordering of songs or phrases can be described by networks with linear segments, forks and bottlenecks within the sequence. The rules for ordering the subunits of birdsong sequences form a species-typical syntax that appears to be innately specified. For example, swamp sparrows, *Melospiza georgiana*, and song sparrows, *Melospiza melodia*, raised without models to copy generate songs that follow species-typical syntax (Marler & Sherman, 1985), and canaries, *Serinus canaria*, that copy syllables from artificial songs with abnormal syntax impose the species-typical syntax on the syllables they learn during development (Gardner, Naef, & Nottebohm, 2005). For some species, the syntactical rules for assembling subunits into song sequences are distinctive to the human ear – for example, the diagnostically different numbers of

repeats of each phrase by different species of North American Mimidae (Borror, 1964).

In species such as the zebra finch, *Taeniopygia guttata*, that most often sing their syllables in a simple linear order, correct phonology develops before correct syntax (Lipkind et al., 2013) and correct syntax does not appear to be important for birds performing song discrimination tasks (Braaten, Petzoldt, & Colbath, 2006; Lawson, Fishbein, Prior, Ball, & Dooling, 2018). In species that sing with a more variable order of subunits, however, syntax appears to be an important factor in defining the animals' responses to a song. Changing the rules for ordering subunits within the vocalizations of California thrashers (Taylor, Brumley, Hedley, & Cody, 2017) and tui, *Prosthemadera novaeseelandiae* (Hill, Brunton, Anderson, & Ji, 2018), affects the responses of males hearing those songs.

Social context is a strong driver of syntax in many vocal communication systems. The presence or absence of conspecifics (and scents of conspecifics) affects how male mice arrange the four syllable types of their vocalizations (Chabout, Sarkar, Dunson, & Jarvis, 2015). Free-tailed bats, *Tadarida brasiliensis*, deliver four syllable types in a variable order and change their syntax in response to playback of vocalizations imitating specific social contexts (Bohn, Smarsh, & Smotherman, 2013) and rock hyraxes, *Procavia capensis*, produce longer vocalizations with more complex syntax as their audience becomes more attentive (Demartsev et al., 2014). Among songbirds, territorial male tui use more complex song syntax during the dawn chorus, when intruder pressure is

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higher, than at other times of day (Hill, Pawley, Anderson, & Ji, 2018), and some birds with two song types, such as field sparrows, *Spizella pusilla*, also sing the more complex song type more frequently at dawn (Nelson & Croner, 1991). Male zebra finches use a fixed linear syntax when courting females but relax the strict ordering of syllables when singing 'undirected' song (Sossinka & Böhner, 1980), and male bobolinks, *Dolichonyx oryzivorus*, sing more syntactically complex songs to other males than they do to females (Ammer & Capp, 1999). Social context can thus trigger changes in the syntax that a singer uses, and variation in syntax may carry information about a particular social context.

The information encoded in context-specific syntax could affect female choice or the outcome of male competition. For example, longer songs sung in the presence of a female demonstrate the energetic reserves available to the courting male, thus indicating his potential quality as a mate (Chabout et al., 2015), and more complex songs are associated with higher extrapair paternity (Hill, Amiot, Anderson, & Ji, 2017). 'High-performance' song attributes deter male intruders (de Kort, Eldermire, Cramer, & Vehrencamp, 2009), and context-specific variation in syntax might operate in a similar fashion.

House finch, *Haemorrhous mexicanus*, songs have a dynamic syntax, in which different paths between syllables can be followed and constituent parts can be rearranged to create different sequences, yielding songs that are more complex than those of many other species that have been the subject of studies of vocal syntax (e.g. 4 syllable types: mice and bats; 4–12 syllable types: zebra finches). In our study population, an individual house finch has a syllable repertoire of 30–65 syllables, assembled into songs averaging 2.3 s and 13.6 syllables in length. There are broad syntactical differences in the organization of different parts of house finch song (Bitterbaum & Baptista, 1979; Mundinger, 1975; Pytte, 1997). The introduction of the song, the most variable segment, is composed of notes or note combinations specific to individuals in the population. The middle of the song includes one of several themes – strings of notes that recur in a relatively stereotyped order. The end of the song, which often concludes with a buzz syllable, also has a more stereotyped order (if songs that stop short are discounted). Within each of the song parts, syllables or groups of syllables may be omitted or inserted, lengthening the sequence, skipping ahead or moving to an alternative phrase.

We asked whether social context affects house finch syllable use, syllable order and song complexity by recording bouts from males singing solo, countersinging with other males, courting females or mate guarding. These contexts are easily observable in the field and touch on important functions of song, including male competition and female choice. Specifically, we predicted that songs sung while countersinging and during courtship bouts would follow different syntactical rules. To test these predictions, we defined a network of transitions between syllables within a song bout, and then used both traditional song measures (such as song length and syllable repertoire) and network measures (such as degree and density of connections) to quantify how songs are assembled.

METHODS

Song Recordings

Male house finches were recorded opportunistically between March and July on the Williams College campus. All recordings were made with a Sennheiser ME66 directional microphone and a Marantz PMD 660 or 661 digital recorder (16 bit, 44 kHz) and sound spectrograms were created with Audacity (audacityteam.org). Birds were recorded for the length of the entire singing bout whenever

possible, and were identified by location (and nest, where appropriate) and the extent and hue of breast coloration. Identification of individuals was confirmed by the presence of distinctive syllable types within the recordings. Songs from 10 individual males that were recorded singing bouts of at least five songs that included four or more syllables (as in Tracy, Zasadny, Erickson, & Siemers, 2009) in at least two different social contexts were used in the analysis, and included 64 bouts (sets of songs separated by more than 1 min), 1179 songs (sets of syllables separated by less than 0.4 s) and 15 989 syllables (continuous sounds in the waveform of a recording).

Social Context

Each bout was assigned to one of four social contexts: solo, countersinging, courtship or mate guarding. Courtship bouts ($N = 9$ bouts, mean $\pm$ SE = 19.0 ± 6.4 songs/bout) included at least one song with a long rising high-frequency 'squeak' syllable or courtship note (Tracy & Baker, 1999; see Fig. 1a) as part of a song and were sung in the presence of a female (within 3 m). Recordings of countersinging bouts (20 bouts, 16.6 ± 2.4 songs/bout) included songs from two nearby males that sometimes overlapped (in two cases, both birds were identified, both birds' song were clear in the recordings, and we analysed both; otherwise we analysed only the focal male's songs). Mate-guarding bouts (5 bouts, 36.0 ± 11.0 songs/bout) were sung by a single male that perched above and more than 3 m away from a female but did not court her. Such bouts ended either when the female flew off and the male followed, or when another male arrived. Solo bouts (30 bouts, 14.1 ± 2.2 songs/bout) were sung by a single male in the absence of other conspecific birds.

Syllable Types

A syllable was defined as a note or cluster of notes that formed a continuous sound in the waveform of a recording. A syllable was considered to be part of a song if less than 0.4 s of silence separated it from another song syllable. Syllables were classified by type, which was designated by a letter corresponding to a cluster of syllables that usually occurred together and a number denoting the identity of a syllable within the cluster, by visually comparing sound spectrograms (Audacity) to an existing syllable type library generated from two decades of song recordings from the local population. When novel syllables were encountered, new syllable types were added to the library. Most syllable types were sung by many individuals, but small variations in frequency and length of the syllable were individually distinctive (see Fig. 1a for examples).

Syllable types were further classified as initial, introductory or main. Initial syllables (light green in Fig. 1) occurred almost exclusively at the beginning of songs. Introductory syllables (purple in Fig. 1) were sung immediately after initial syllables, were relatively short (135 ± 4 ms, including the silent interval preceding the syllable) and were delivered in an order that usually varied between birds. Main syllables (other colours in Fig. 1), sung during the middle and end of songs, were relatively long (225 ± 10 ms) and included syllable clusters that maintained the same order in different birds' songs.

Songs that were illegible due to background noise were excluded from the analysis. In addition, some overlapping songs from two countersinging birds within a recording were indistinguishable from one another and were also excluded from the analysis. Excluding overlapping songs could result in underestimation of variability in a house finch's syntax and repertoire in the context of countersinging. However, as described in the analysis

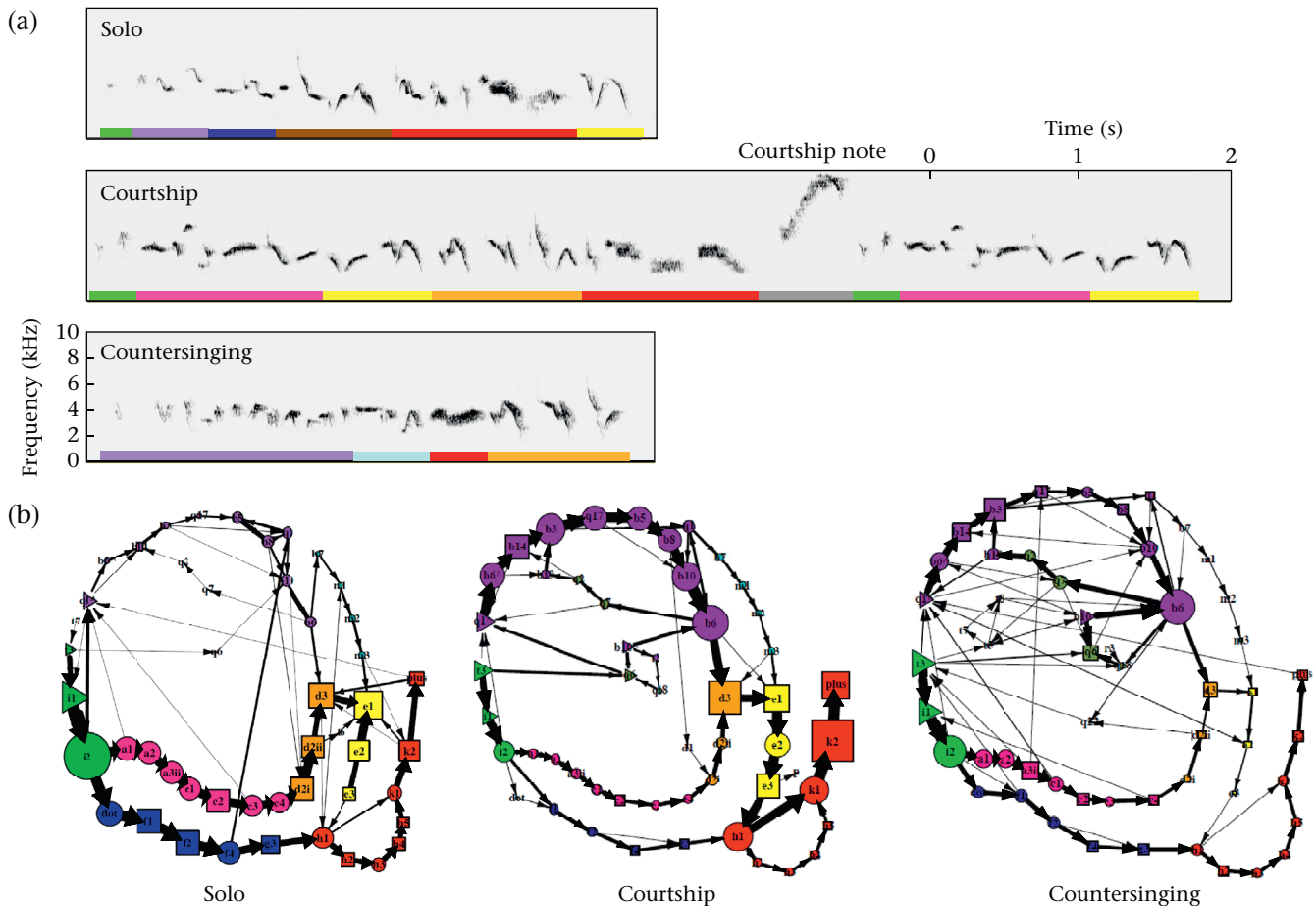


Figure 1. Examples of house finch songs and bouts in different social contexts. (a) Sonograms of songs recorded by males while singing solo song, while courting females (determined by the presence of a female and by the presence of a high-frequency courtship note within a song bout) and while countersinging with another male. Colours denote phrases (sets of identified syllable types that consistently co-occur), with introductory syllable phrases in purple, initial syllables in green, and common distinctive main phrases in other colours. The examples are drawn from recordings of different males; most syllable types are sung by many males within the population. (b) Network diagrams showing transitions (arrows) between syllables (nodes) for three bouts sung by one male in different social contexts. Line width and symbol size are proportional to frequency of the transitions and syllables within the bout. Colours of symbols denoting syllables correspond to colours in (a). Solo bout = 60 songs, courtship bout = 56 songs, countersinging bout = 47 songs.

section, we corrected for sample size, both to address this issue and that of differences in bout length and number of songs recorded.

Each bout was transcribed as a series of syllable sequences corresponding to individual songs, and these sequences were converted into lists of transitions and syllables as well as a transition matrix for further analysis.

Analysis

Song complexity

We used the following traditional measures of song complexity to characterize bouts sung in different social contexts.

Syllable type repertoire. The number of unique syllable types sung in a bout.

Transition type repertoire. The number of unique transitions between syllables sung in a bout.

Song length. The length of a song, measured in time (seconds) or in number of syllables. We measured song length both including and excluding courtship notes, which are particularly long and sung only in one social context.

Average syllable length. The length of the song (in seconds) divided by the number of syllables in the song (thus the average syllable

length also included the average leading silent interval, except for the first note of the song). Here again we measured average syllable length both including and excluding courtship notes (and their leading silent intervals).

Sequence consistency. The number of typical transitions divided by the total number of transitions (Scharff & Nottebohm, 1991). Typical transitions are defined as the most common transitions leading from each syllable.

Network diagrams and measures

Traditionally, birdsong syntax has been diagrammed with flow charts or network diagrams showing the sequential order of songs or syllables (e.g. Sossinka & Böhner, 1980). In such diagrams, vertices (nodes) represent syllables and lines (edges) represent transitions between the syllables (see Fig. 1b). Such charts are helpful in visualizing patterns in complex songs and long bouts such as those sung by house finches. The underlying networks linking syllables via transitions can be subjected to network analyses similar to those that are applied to social networks. Such network analyses have been applied to nightingale song (Weiss et al., 2014), where the 100–200 song types that a bird may sing (Berwick, Okanoya, Beckers, & Bolhuis, 2011) were the nodes, and to mice (Chabout et al., 2015), where five types of calls were the

nodes. We analysed our recordings of house finch song, with 20–60 syllable types per bout, using the following network measures to assess the complexity of the transition networks linking syllable types.

Average degree. The average number of transitions for the syllables within a bout. A syllable that always occurred between the same leading and following syllables would have a degree of 2. A syllable that always occurred in the initial position and was always followed by the same syllable would have a degree of 1.

Density. The number of transitions between syllables that occurred in a bout as a proportion of the total number of possible transitions.

Simple paths. The number of the possible strings of syllables that could be sung – given the transitions between syllables that a bird sang in a bout, and omitting repeated syllables or loops. A high number of simple paths represents increased variability in syntax. The number of simple paths was calculated using the igraph package (Csárdi & Nepusz, 2006) within R (www.R-project.org, v.3.3.2). Strings that were subsets of longer strings were not included in the measure.

Although density and simple paths measure similar aspects of syntax complexity, the number of simple paths is more sensitive to the location of transitions within the network. Fig. 2 illustrates these measures for simple examples of song syntax networks. Although the omission of loops and repeated sequences may reduce the potential variability that can be represented by the simple paths measure, repeated syllables are rare within the repertoires of the Williams College house finch population. Most birds' transition repertoires contained no repeated syllables or one syllable that was occasionally repeated; one bird repeated two syllables.

Statistical Analysis

We used linear mixed-effects models to assess the effect of social context on song complexity and syntax measures with the lme4 package (Bates, Mächler, Bolker, & Walker, 2015) in R (www.R-project.org). We first transformed (natural logarithm) the variables that were not normally distributed (simple paths, number of songs in a bout and network density). We then tested whether the season of the recording (early, 12 March–21 April, versus late, 25 May–7 July) was related to differences in the song and syntax measures. For only one variable, the proportion of the main syllables in the song, did this relationship approach significance, and so we included season of recording as a random effect variable only within the model testing the effect of social context for the proportion of main syllables in the song. We also asked whether the number of songs in a bout was related to the measures of song and syntax. Several variables (simple paths, degree of all syllables, degree of introductory syllables, degree of main syllables, syllable type repertoire and transition type repertoire) were significantly

related to the number of songs per bout after correcting for multiple tests, and so we included the number of songs per bout as a random effect variable in models assessing the effect of social context on those measures. The identity of the singer was also included as a random effect in all analyses, as individual birds differed in their repertoires. To account for the fact that we tested the effect of context on 10 song variables, we set the criterion for significance at $P < 0.005$, and then performed post hoc tests (Tukey's contrasts) to compare contexts for models that reached significance.

To determine which measures best differentiated the social context in which bouts were sung, we performed linear discriminant function (LDF) analyses using the R packages flipMultivariates (github/Displayr/flipMultivariates) and MASS (cran.r-project.org/web/packages/MASS). We excluded mate-guarding bouts because the sample size for that social context was small (the resulting sample size was 59 bouts). We asked how effectively the social context of bouts could be classified based on measures of song structure and syntax. We used Wilks' λ and chi-square tests to assess the significance of linear discriminant analyses and their ability to predict social context more often than expected by chance. After identifying the variables that best discriminated the three social contexts, we randomly split the data set into training bouts (70%) and test bouts (30%) and used the results of an LDF performed on the training bouts to predict the context of the test bouts, repeating this process 10 000 times with different random subsets of the data used as training and test bouts.

Ethical Note

Animals were not captured as part of this study, which was approved by the Institutional Animal Care and Use Committee of Williams College (IACUC protocol WH-B-2015). The study site is a college campus with heavy foot traffic; birds nested over the entrances and under the eaves of buildings and sang both from buildings and from nearby trees. Recordings were made from sidewalks and grassy areas frequented by pedestrians. We did not observe any nest desertion.

RESULTS

Syllables, Transitions and Social Context

Transition type repertoire varied across bouts sung in different social contexts ($F_{3,60} = 6.41$, $P < 0.001$; Fig. 3b), but syllable type repertoire did not ($F_{3,60} = 2.18$, $P = 0.1$; Fig. 3a). Post hoc tests showed that countersinging bouts included (on average, after correcting for singer and number of songs in the bout) 17.5 more transition types than solo bouts ($P < 0.001$). Although the sample size was smaller, mate-guarding bouts also had more transition types than solo bouts (24.0 more; $P < 0.05$). On

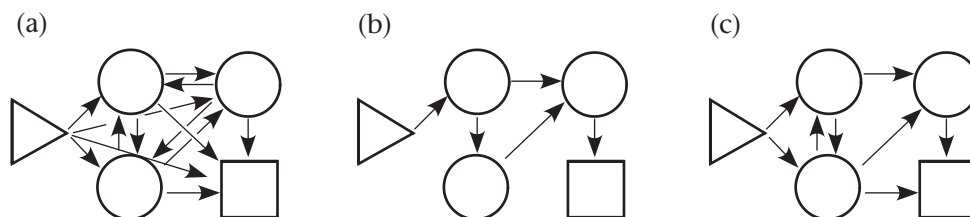


Figure 2. Song syntax measures illustrated with simple syllable/transition networks. In this simple example, a 'start' syllable is shown with a triangle and an 'end' syllable with a square, and internal syllables with circles; arrows show transitions between syllables (in this simple example, all songs must have one internal syllable, and start and end syllables do not also serve as internal syllables (although they frequently do in actual house finch songs)). (a) The complete network, with the 13 specified transitions (the number of possible transitions is 20; average degree = 5.2, density = 0.65, simple paths = 16, assuming no path reversals). (b) A simple syntax network with one fork, at the first internal syllable (average degree = 2.0, density = 0.25, simple paths = 2). (c) A more complex syntax network (average degree = 3.2, density = 0.40, simple paths = 6).

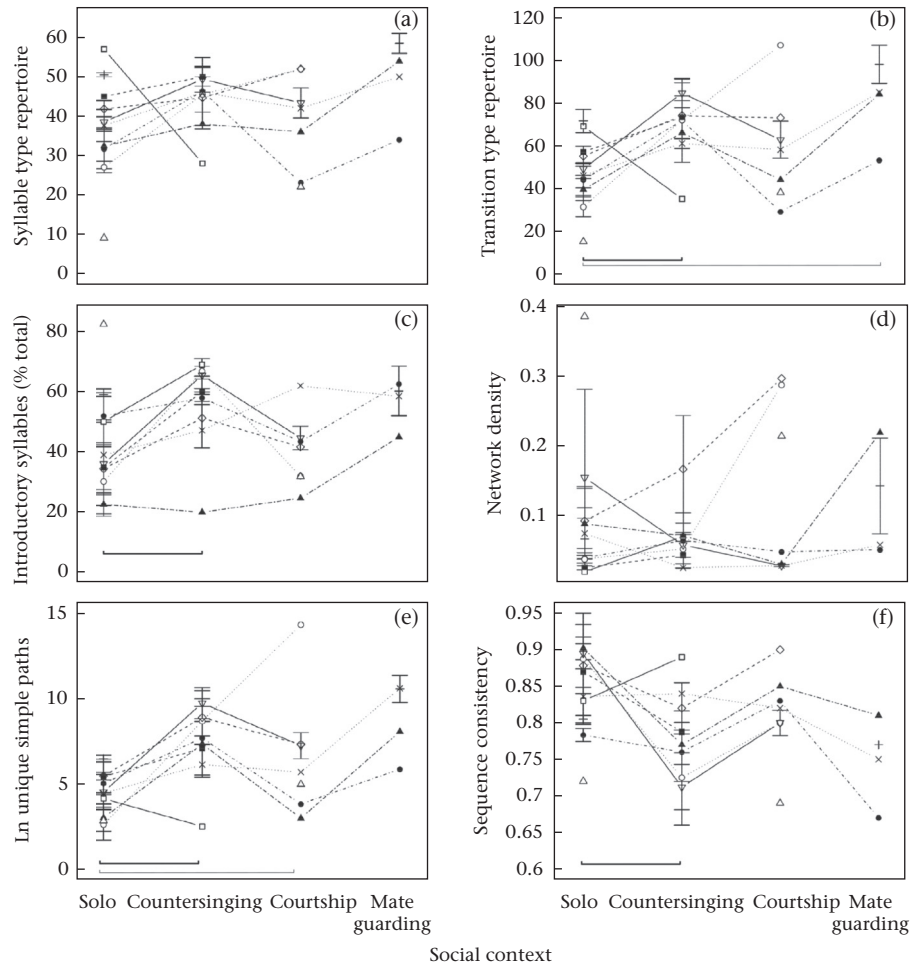


Figure 3. Song syntax measures as a function of social context: (a) number of syllable types within a bout, (b) number of transition types within a bout, (c) percentage of syllables within a bout that were introductory syllable types, (d) network density (a measure of interconnectedness within the network defined by the transitions between syllables), (e) number of unique simple paths (possible routes through a network from a start syllable to an end syllable) within the network defined by the transitions between syllables in a song bout and (f) sequence consistency within a bout (the proportion of transitions that were the most common transitions from each syllable). Individual birds are denoted by different symbols and line types; where multiple bouts were recorded for a single bird and a given social context, 95% confidence intervals are shown with error bars. Brackets denote statistically significant differences between two social contexts (thick lines = $P < 0.001$; thin lines = $P < 0.05$).

average, after correcting for singer and number of songs, courtship bouts had 6.9 fewer transitions than countersinging bouts and 9.6 more transitions than solo bouts, but neither of these differences reached significance in post hoc tests.

The proportion of introductory syllables within songs also varied with social context ($F_{3,60} = 5.99$, $P < 0.005$; Fig. 3c). Countersinging males included a larger proportion of introductory syllables in their bouts than did males singing solo bouts (post hoc test: $P < 0.001$) or courtship bouts (post hoc test: $P < 0.05$). Although mate-guarding bouts included a high proportion of introductory notes, they did not differ significantly from solo bouts (the mate-guarding sample size was relatively small).

Thus, social context did not affect the number of syllable types that a male sang, but males singing to other males or guarding mates sang more transition types. Countersinging males also included a larger proportion of introductory notes (and thus a correspondingly smaller proportion of main notes) in their songs.

Measures of Syntax Complexity

Sequence consistency, the ratio between the number of times the most common transition leaving each syllable is used and the total number of transitions, describes how fixed song syntax is within a

bout. Sequence consistency varied with social context ($F_{3,60} = 6.98$, $P < 0.001$; Fig. 3f). Males singing solo bouts sang with significantly greater sequence consistency than did males that were countersinging (post hoc test: $P < 0.001$) or mate guarding (post hoc test: $P < 0.01$), but they did not differ from males singing courtship bouts (post hoc test: $P = 0.53$). This variation in consistency was also reflected in the number of unique simple paths within bouts ($F_{3,60} = 8.56$, $P < 0.001$; Fig. 3e). Countersinging bouts included significantly more simple paths than did solo bouts (post hoc test: $P < 0.001$), and both mate guarding (post hoc test: $P < 0.05$) and courtship bouts also had more simple paths than solo bouts (post hoc test: $P < 0.05$). However, network density, the ratio between transitions actually sung and possible transitions, did not differ with social context ($F_{3,60} = 1.21$, $P = 0.33$; Fig. 3d), and appears to be a less sensitive measure of syntax variability than sequence consistency and the number of simple paths, which vary consistently with social context and indicate that countersinging songs have a less fixed/more complex syntax.

Degree (transitions per syllable)

The average number of transitions per syllable (= 'average degree' in network measures) is also related to syntax complexity; as the number of transitions per syllable increases, so does the

potential for decreased consistency and increased number of simple paths. The average degree for all syllables within a bout was sensitive to social context ($F_{3,60} = 7.92$, $P < 0.001$; Fig. 4a). Countersinging bouts had higher average degree than solo bouts (post hoc test: $P < 0.001$), and solo bouts also had lower average degree than mate-guarding (post hoc test: $P < 0.05$) and courtship bouts (post hoc test: $P < 0.05$). However, introductory syllables had a significantly higher average degree than main syllables (paired t test: $t_{63} = 8.37$, $P < 0.001$; cf. Fig. 4b and c). The change in introductory note degree with song context paralleled the overall change in degree ($F_{3,60} = 7.64$, $P < 0.001$), with solo bouts having a significantly smaller average degree than courtship bouts (post hoc test: $P < 0.001$). Different social contexts were also associated with differences in the average degree of main syllables ($F_{3,60} = 4.51$, $P < 0.01$), and here the post hoc analysis found that the degree of main syllables was higher for courtship bouts than for solo bouts ($P < 0.05$). Thus, the average degree of introductory syllables increased substantially and significantly in countersinging bouts, and the average degree of main syllables had a smaller but still significant increase in courtship bouts.

Song length

Song length varied with social context, whether or not the long courtship notes were included in measurements and whether song length was measured in seconds (with courtship notes: $F_{3,60} = 18.62$, $P < 0.001$; without courtship notes: $F_{3,60} = 15.68$, $P < 0.001$; Fig. 5a) or syllables (with courtship notes: $F_{3,60} = 12.26$, $P < 0.001$; without courtship notes: $F_{3,60} = 10.64$, $P < 0.001$; Fig. 5b). For both measures, songs in courtship bouts were significantly longer than songs in all other contexts (post hoc test: $P < 0.001$, for seconds, whether or not courtship notes were included) and had more syllables (post hoc test: $P < 0.01$, whether or not courtship notes were included). Countersinging bouts had more syllables than solo bouts (post hoc test: $P < 0.05$). We excluded courtship notes (which are long and restricted to one context) when comparing average syllable length, which also varied with context ($F_{3,60} = 34.14$, $P < 0.001$; Fig. 5c). Post hoc tests showed that courtship bouts used longer syllables than countersinging and mate-guarding bouts ($P < 0.001$) as well solo bouts ($P < 0.05$). Solo songs used longer syllables than both courtship bouts and countersinging bouts ($P < 0.001$).

Within courtship bouts, some songs had courtship notes while other songs did not. We compared the lengths of these two categories of songs (courtship note 'present' and 'near' courtship note) to solo songs (courtship note 'absent'). Song length differed across categories, both when it was measured in seconds ($F_{2,61} = 138.3$, $P < 0.001$; excluding the length of the courtship note: $F_{2,61} = 72.8$, $P < 0.001$; Fig. 5d) and when it was measured in syllables ($F_{2,61} = 73.9$, $P < 0.001$; without courtship notes: $F_{3,60} = 55.9$, $P < 0.001$; Fig. 5e). Songs with courtship notes were significantly longer and had more syllables than other songs in the courtship bout or songs in solo bouts (post hoc test: $P < 0.001$, with or without courtship notes). When song length was measured in seconds, songs in courtship bouts that were near courtship notes but did not include them were longer than songs in solo bouts (post hoc test: $P < 0.01$, with or without courtship notes). Average syllable lengths also varied with the presence of courtship notes ($F_{2,61} = 38.9$, $P < 0.001$, when courtship notes were included; Fig. 5f). Songs with courtship notes had longer syllables than nearby songs in the same bouts, and songs in solo bouts had shorter syllables than both types of songs in courtship bouts (post hoc test: $P < 0.001$). However, when courtship notes were excluded from measurements of average syllable length, only the differences between

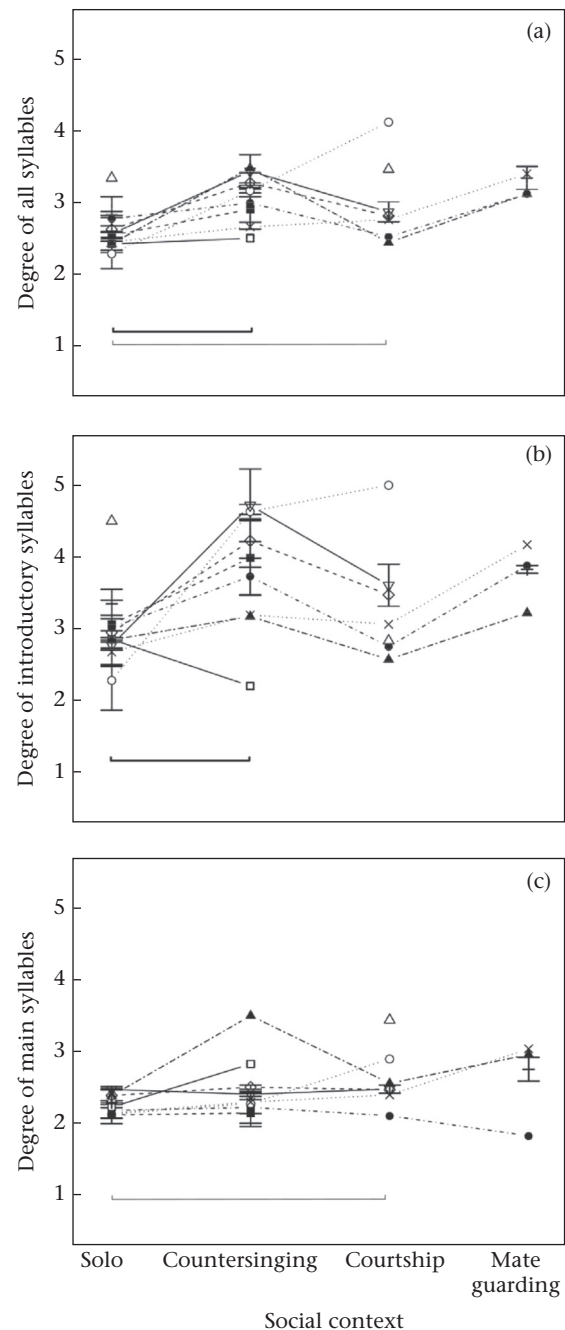


Figure 4. Average number of transitions associated with a syllable ('average degree') in different social contexts for (a) all syllables, (b) introductory syllables and (c) main syllables. (Note: a syllable that was always preceded and followed by the same syllable would have a degree of 2.) Individual birds are denoted by different symbols and line types; where multiple bouts were recorded for a single bird and a given social context, 95% confidence intervals are shown with error bars. Brackets denote statistically significant differences between social contexts (thick lines = $P < 0.001$; thin lines = $P < 0.05$).

solo songs and either songs near courtship note songs or songs containing courtship notes remained significant (overall: $F_{2,61} = 14.5$, $P < 0.001$; post hoc test: $P < 0.05$, for solo songs versus songs including or near courtship notes).

Finally, we asked whether songs surrounding courtship note songs within courtship bouts varied in length based on their position relative to courtship note songs (Fig. 6). There were no significant differences between songs preceding courtship note

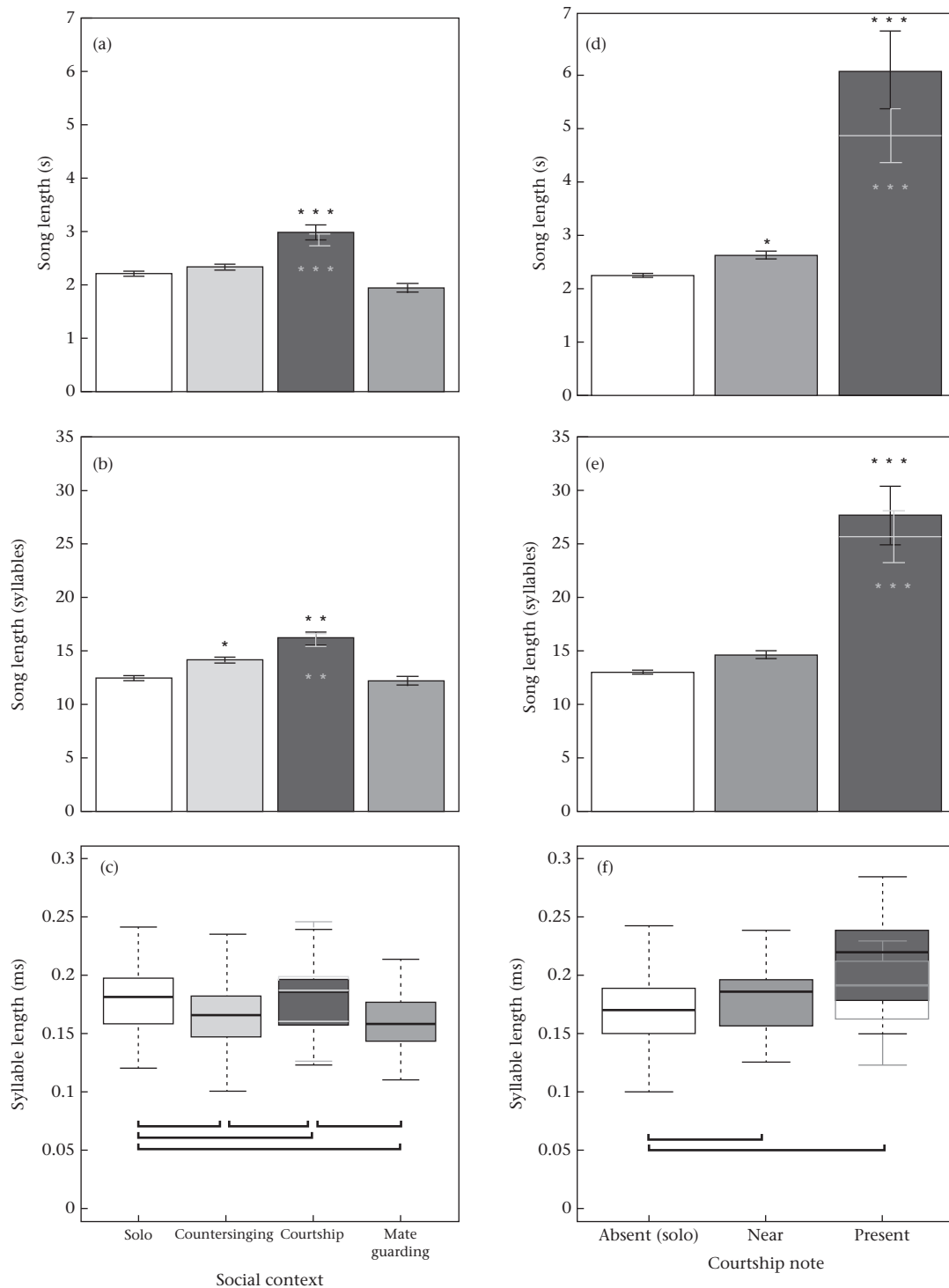


Figure 5. Song length, in seconds (a) and syllables (b), as well as syllable length (c), for bouts sung in different social contexts. (d, e, f). The same measures compared for songs within solo bouts (courtship notes absent), songs within courtship bouts that lacked courtship notes (near) and songs within courtship bouts that included courtship notes (present). Because courtship notes are long, values for song length and syllable length after excluding courtship notes were also calculated and are shown in grey for courtship social context (a, b, c) and for courtship note present (d, e, f). For (a, b, d, e), error bars denote the 95% confidence interval. For (c, f), the median and 25% and 75% range of the distribution is shown by the boxes, and the 5%–95% range is shown by the whiskers. Brackets (thick lines = $P < 0.001$; thin lines = $P < 0.05$) below the box plots denote differences between syllable lengths for different groups when the long courtship notes were excluded from the analysis. *Groups that had longer songs than solo bouts ($P < 0.05$). **Groups that had longer songs than all other groups ($P < 0.01$). ***Groups that had longer songs than all other groups ($P < 0.001$).

songs and those following courtship note songs in song length, number of syllables or average syllable length (post hoc tests: $P > 0.05$, after correcting for multiple tests).

To summarize, courtship bouts had longer songs, more syllables and longer syllables than bouts sung in other social contexts, even

after correcting for the fact that the courtship note is a very long syllable. Within courtship bouts, songs with courtship notes were longer and had more and longer syllables than both songs in solo bouts and songs in courtship bouts that did not include courtship notes. Courtship bout songs that did not include courtship notes

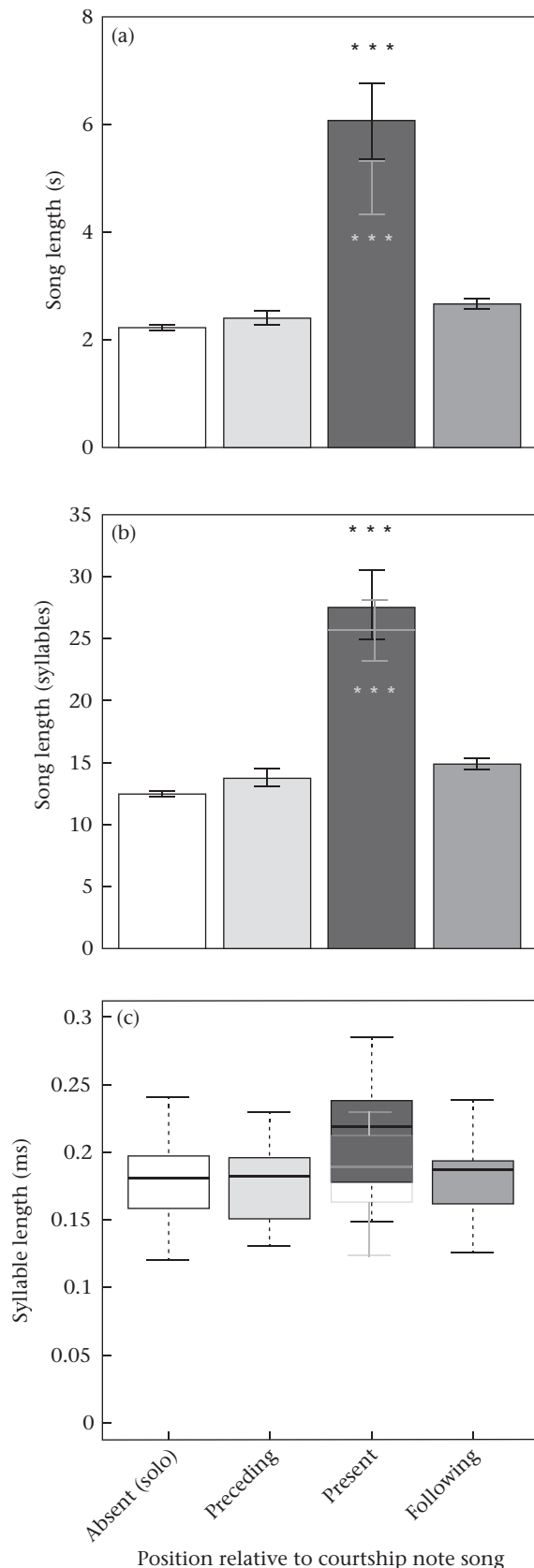


Figure 6. Position within a courtship bout and song length. Song length, as measured (a) in seconds, (b) by the number of syllables as well as (c) the mean syllable length for songs in solo bouts as compared to courtship bout songs that preceded, included or followed courtship notes. Because courtship notes are long, values for song and syllable length after excluding courtship notes were also calculated and are shown in grey

were longer and had longer syllables than songs in solo bouts, but differences between songs preceding and following courtship note songs were not significant.

Linear discriminant analyses

To assess the relative importance of song measures for distinguishing among different social contexts, we used linear discriminant analyses ($N = 59$ bouts; the mate-guarding context was omitted because of small sample size). When we used the full set of nine song measures we had previously identified as being related to social context (unique simple paths, degree, degree of introductory syllables, degree of main syllables, syntax consistency, syllable types, transition types, proportion of introductory syllables and mean song length), the analysis correctly classified 83% of bouts (Wilks' $\lambda = 0.35$; $\chi^2_4 = 56.4$, $P < 0.001$). The number of unique simple paths explained more of the variance than any other variable ($R^2 = 0.37$, $P < 0.001$) and best discriminated countersinging bouts from other bouts. Number of transition types ($R^2 = 0.31$), number of syllable types ($R^2 = 0.14$), overall degree ($R^2 = 0.32$), degree of introductory syllables ($R^2 = 0.32$) and proportion of introductory syllables ($R^2 = 0.23$) also significantly discriminated countersinging bouts from other contexts and loaded onto the first discriminant dimension along with unique simple paths. Syntax consistency best discriminated solo bouts from other social contexts ($R^2 = 0.24$, $P < 0.001$). Mean song length best discriminated female-directed bouts from other social contexts ($R^2 = 0.21$, $P < 0.001$), as did, although more weakly, the degree of main song syllables ($R^2 = 0.12$). A linear discriminant analysis using only unique simple paths, syntax consistency and song length accurately classified 71% of the bouts (Wilks' $\lambda = 0.46$; $\chi^2_4 = 27.5$, $P < 0.001$). When we then used the three variables that best predicted each social context (unique simple paths, syntax consistency, mean song length) to train the LDA to discriminate among a random subset consisting of 70% of the bouts sung in each social context, it correctly classified 69.7% (average of 10000 trials) of the remaining 30% of the bouts.

DISCUSSION

Social context affected several aspects of overall song syntax in house finches. Song syntax was most complex in countersinging bouts. Linear discriminant analyses identified syntax consistency as characterizing solo bouts and a high number of unique simple paths as the best predictor of countersinging bouts (a high overall degree, a high degree of introductory syllables and a large number of transition types, all measures associated with syntax variability, also strongly predicted the countersinging context). Longer songs characterized courtship bouts. These differences in the syntax of solo and countersinging bouts were not driven by the use of a larger syllable repertoire, as the number of syllable types sung did not differ between solo and countersinging bouts.

A closer look at the pattern of introductory syllable sequences in countersinging bouts reveals that the increase in syntax variability in countersinging bouts was largely due to males singing more introductory syllables and using more transitions between those syllables. The effect on song syntax of singing more introductory syllables with higher average degree was to create more branching points within the introductory segment of the song (illustrated in

for courtship note present songs. For (a, b), error bars denote the 95% confidence interval. In (c), the median and 25% and 75% range of the distribution is shown by the boxes, and the 5%–95% range is shown by the whiskers; there were no differences in average syllable length between groups when courtship notes were excluded. ***Groups that had longer songs than all other groups ($P < 0.001$).

Fig. 1b) and to use those branching points more frequently, yielding a longer introductory segment with a more variable syntax.

The increase in syntactical variation achieved by singing longer introductory segments with more transition types per introductory syllable might be due to a number of mechanisms. One possibility is that such variability is a display of complexity that deters other males seeking extrapair copulations (Hill, Brunton et al., 2018). Alternatively, males engaged in countersinging might be using a special form of song matching (song matching is reviewed in Searcy & Beecher, 2009). Pre-emptive matching focuses upon predicting the other male's next song or syllable and anticipating that utterance by altering the vocal sequence (Hedley, Denton, & Weiss, 2017; Todt & Naguib, 2000). Such anticipatory syllable matching would lead to a male singing atypical and novel transitions between syllables as he jumps ahead or back within his normal syllable sequence.

Although house finches defend an area around their nest and guard their mates with behaviours such as chasing other males away, they are not strongly territorial, allowing other pairs to nest within as little as a few feet away (Thompson, 1960), and where extrapair paternity has been measured, it has been low (Mennill, Badyaev, Jonart, & Hill, 2006). Because proximity is common, it is possible that male–male interactions in house finches are not necessarily competitive. One possibility is that countersinging may be a cooperative performance, potentiating the ability of either individual male to deter other males or to attract females. To test such competition and cooperation hypotheses, analyses of syllable matching in playback studies and in bouts where two countersinging males' songs are clearly recorded would be useful.

Measures of overall syntax in mate-guarding bouts were similar to those for countersinging bouts, suggesting that the emphasis during mate guarding is on male–male interactions. However, the small sample size precluded some of these trends from reaching significance.

Courtship song syntax differed from solo bouts and from countersinging bouts. Courtship bouts had more simple paths than solo bouts but did not differ from solo bouts in syllable or transition repertoires, in sequence consistency or in overall density. However, the main syllables (middle and end song segments) of courtship song had a higher degree (more connections to other syllables) than did those of solo song, which produces a higher number of simple paths. Although this increase in degree was not as large as for the introductory syllables of countersinging bouts, it did reach significance after correcting for number of songs sung and multiple comparisons.

The most salient difference between songs in courtship bouts and songs delivered in other social contexts was increased song length – whether measured in seconds, syllables or average syllable length. Mean song length discriminated courtship bouts from other social contexts better than any other song measure. The increase in length was primarily due to the songs that included courtship notes: such songs were often compound songs (see example in Fig. 1a) that were more than twice as long as songs sung in solo bouts and included more long syllables. Songs sung during courtship bouts that did not include courtship notes were still longer and had more syllables than songs sung in solo bouts, but they were shorter and had shorter syllables than courtship note songs. Whether a song was sung soon before or soon after a courtship note song did not have a clear effect on song or syllable length.

When presented with recorded songs of male house finches in a captive setting, females preferentially approached speakers playing longer songs or songs separated by shorter silent intervals (Nolan & Hill, 2004). In the field, males that sang longer songs initiated their first clutch earlier in the season (Mennill et al., 2006). Longer songs

are likely to be an honest signal of good genes because singing requires high levels of energy, as demonstrated in great tits, *Parus major*, where song length predicts male quality (Lambrechts & Dhondt, 1986). We show that males sing the longest versions of their songs in the context of courtship, and that in this social context they lengthen their songs by forming compound songs that repeat middle and end syllables without substantially altering overall syntax patterns. Female house finches may prefer both (1) longer songs and (2) songs that maintain the species- and population-typical structure – as do female starlings, *Sturnus vulgaris* (Gentner & Hulse, 2000).

When syntax varies with social context, there may be a trade-off between signalling about social context and signalling about species identity using species-typical syntax. Such a trade-off may have important consequences during periods of range expansion. House finches were introduced into the eastern United States in the 1940s (Elliott & Arbib, 1953), and then expanded their range westward; they now inhabit all of the contiguous United States (Sauer et al., 2014). Range expansion represents a form of population bottleneck, with founders being relatively few in each newly colonized area. Lachlan et al. (2013) described the effects of a series of such bottlenecks on the song syntax of chaffinches, *Fringilla coelebs*, that colonized a chain of islands. Species-specific syntax decreased after each successive colonization event. During rapid range expansion, interactions between male house finches might act to break down species-typical syntax by increasing the importance and syntax variability of introductory syllables, while female choice might operate to maintain the overall structure of songs by favouring repeated sequences of main syllables. However, the overall syntactic structure of the songs of the original western population of house finches and that of the introduced eastern population are similar (Bitterbaum & Baptista, 1979; Mundinger, 1975; Tracy et al., 2009), and so rules for assembling songs do not appear to have been relaxed as a consequence of the population bottleneck.

During courtship, males sing longer songs that are often compounds of sequences of main syllables – suggesting that, for females, both the amount of song and the use of main song syllables with more stereotyped syntax is important. In contrast, countersinging bouts involving more than one male are marked by increased diversity in the syntax of an individual male's song, and an expansion of the introductory segment. Thus, males appear to tailor their songs to the social context, and so to the type of sexual selection that is likely to be operating. Overall, these results suggest that female choice favours both long songs and a stable species-typical syntax, whereas male–male interactions act to increase syntactic diversity.

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